

## A NOTE ON REPRODUCTIVE PHENOMENA IN SOME LIZARDS.

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(Three Text-figures.)

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### I. THE PLACENTATION OF *Lygosoma (Hinulia) quoyi*.

In a preliminary note communicated to this Society, 30th March, 1927, the author recorded the occurrence of placentation in the Scincid lizards *Lygosoma (Hinulia) quoyi*, *Egernia whitei* and *Egernia striolata* and stressed the importance of the discovery of a type of allantoplacentation in these lizards which more closely resembles that found in the Mammalia than any hitherto recorded in a reptile. It is proposed in the present communication to describe briefly the allantoplacentation of *L. quoyi* and compare it with allantoplacentation as it occurs among the Reptilia, Marsupialia and Eutheria and to follow at a later date with a detailed account of the placentation of *L. quoyi*, *E. whitei* and *E. striolata*.

#### 1. DESCRIPTION OF MATERIAL.

The habitat of *L. quoyi* ranges from sea level to approximately 5,000 feet above sea level. Those lizards which inhabit the highest regions are much smaller in the adult condition than those found at sea level, and during the gestation period, which covers approximately three months, the females of the former type carry from three to five young, while those of the latter carry from five to nine young. The placentae in both are identical.

Given normal climatic conditions, ovulation among the females at sea level (Sydney, N. S. Wales) occurs during the beginning of October, whereas it is two or three weeks later among the females at 5,000 feet above sea level. There is no sign of albumen surrounding the egg, but a thin shell membrane is present during the early stages of development of the embryo. However, by the time the chorio-allantoic membrane is well established, there is comparatively little shell membrane

left between it and the uterus. The developing embryo is dorsal in position with regard to the parent and lies with its head directed mesially whether the embryo be in the right or left oviduct, the embryos in the one female being approximately at the same stage in their development. The uterus surrounds each egg as a thick white envelope which remains as an expanded chamber on the extraction of the egg. These chambers are connected each to each by a short narrow straplike portion of the uterus. Before the formation of the placentae the wall of each of these so called "incubatory chambers" is uniform in structure throughout and consists of an outer covering of peritoneum, a coat of longitudinal and circular muscle and a narrow mucous membrane with flattened glands embedded, bounded by a layer of fairly large columnar epithelial cells. The chorion lies immediately beneath the uterus and consists of an outer layer of small flat ectoderm cells and an inner layer of tapering mesoderm cells. The allantoic stalk carrying the allantoic vessels leaves the ventral surface of the body of the embryo a short distance in front of the hind limbs, passes upwards around the embryo and expands into the allantoic vesicle. The mesoderm bounding the outer surface of the allantois fuses with that of the chorion forming the chorioallantoic membrane in the connective tissue of which ramify the allantoic vessels. The fusion between the allantois and the chorion gradually extends around the under surface of the chorion until the allantois reaches the yolk-sac. As in *Lygosoma (Lirolepisma) entrecasteauxi* (Harrison and Weekes, 1925) the allantois does not extend around the yolk-sac but comes into contact with the upper surface only, the mesoderm of the allantois fusing with that of the yolk-sac.

The omphaloplacenta is insignificant and functions during the early development of the embryo. It is composed of modified uterine epithelium and chorionic ectoderm overlying a richly vascular yolk-sac.

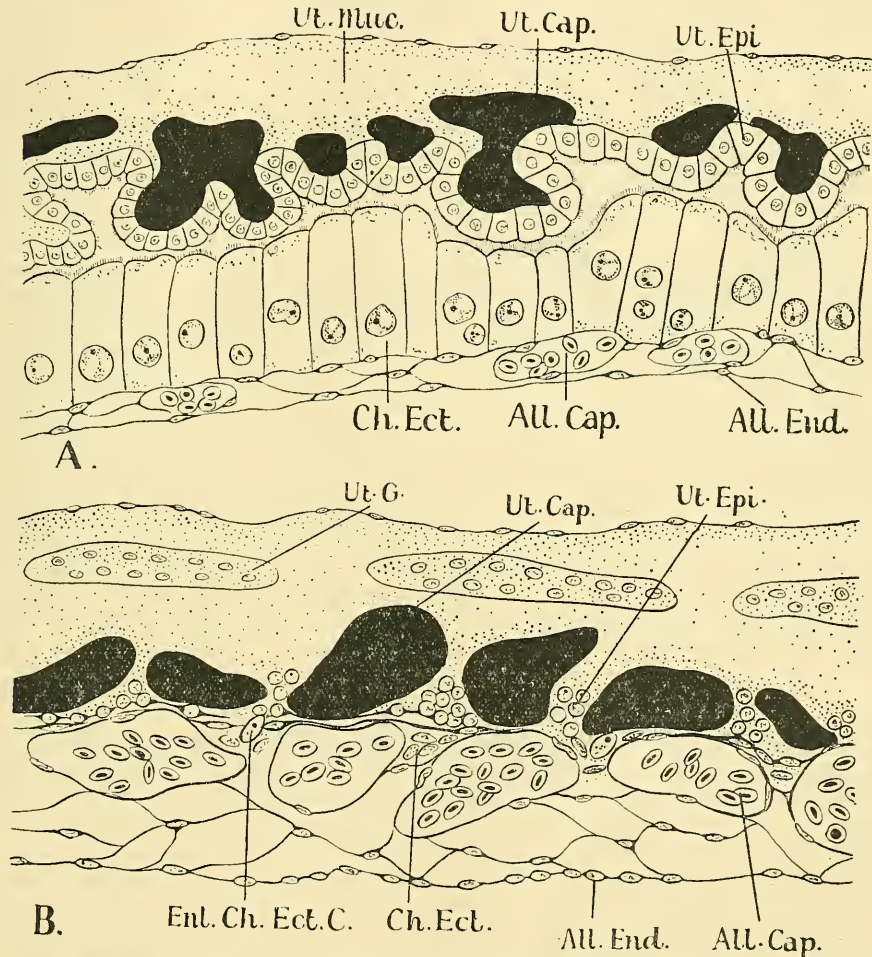
The allantoaplacenta is highly specialized, is established approximately two weeks after fertilization, reaches maturity two weeks later and functions until immediately prior to the birth of the foetus. The fixation of the embryo is brought about by the invasion of the uterine epithelium by enlarged chorionic cells scattered throughout the chorionic ectoderm. The development of the placental region is not restricted, placental modifications of maternal and foetal tissues existing for the main part over the entire area embraced by the allantois.

In the modification of the maternal tissues, the uterine epithelium undergoes partial degeneration, the dividing cell walls disappearing and the cell nuclei becoming pushed aside by the multiplication and expansion of the underlying maternal capillaries, so that they come to be roughly grouped in nests between the exposed capillaries (Text-fig. 1, B). The chorionic ectoderm consists of the scattered and enlarged cells which serve to fix the chorioallantoic membrane in position, and for the remainder, of a layer of flattened cells which undergo the same partial degeneration on the expansion of the underlying allantoic capillaries as occurs among the uterine epithelial cells. Neither the uterine epithelial cells nor the chorionic ectoderm cells completely disappear but remain clearly definable throughout the life of the placenta, the former functioning for food secretion and the latter for food absorption (Text-fig. 1, B). But the function of food transition is mainly carried on by the closely apposed maternal and foetal capillaries, which are for the most part only separated by their endothelial walls and a thin layer of maternal and foetal cytoplasm. This type of allantoaplacentation is extremely interesting and is so far peculiar to this species of lizard, having no parallel among those reptiles for which placentation has been recorded.

2. COMPARISON WITH *Chalcides tridactylus*, *Lygosoma entrecasteauxi* AND *Tiliqua scincoides*.

Definite placentation amongst lizards has been described in *Chalcides tridactylus*, *Chalcides ocellatus* by Giacomini (1891 and 1906 respectively); in *Tiliqua scincoides* by Flynn (1923); in *Lygosoma entrecasteauxi* by Harrison and Weekes (1925).

In both the classic *C. tridactylus* and *L. entrecasteauxi* the allantoplacental area is restricted and elliptical in shape, and the uterine wall is folded into villous ridges lined by enlarged cubical ciliated epithelial cells and containing a



Text-figure 1.—The two dissimilar types of reptilian allanto-placentation. (A) section through placental region of *L. entrecasteauxi* showing modification and apposition of maternal and foetal epithelium; (B) section through placental region of *L. quoyi* showing partial degeneration of maternal and foetal epithelium. All. Cap., Allantoic Capillary; All. End., Allantoic Endoderm; Ch. Ect., Chorionic Ectoderm; Enl. Ch. Ect. C., Enlarged Chorionic Ectoderm Cell; Ut. Cap., Uterine Capillary; Ut. Epi., Uterine Epithelium; Ut. Muc., Uterine Mucosa.

rich network of maternal capillaries. The chorionic ectoderm cells are columnar, extremely elongated and in *L. entrecasteauxi*, ciliated. There is no interpenetration of chorionic ectoderm into the maternal crypts, the fixation of the embryo being so slight that the least handling in the preparation of material separates the maternal and foetal membranes (Text-fig. 1, A). As Flynn (1923, p. 76) possessed but one stage in the development of the allantoplacenta of *T. scincoides* and further, as his account is extremely brief and without the necessary illustrations, it is impossible to deduce correctly the type of allantoplacentation present in that lizard. He says (1923, p. 76) that "the union between chorion and uterine epithelium is very intimate. The uterine epithelium apparently consists of a single layer of very flattened cells, while the chorionic ectoderm has proliferated greatly, is much vacuolated, resembling a typical plasmodium, and is formed in the main of markedly enlarged cells with large nuclei and connected together by amoeboid processes. These processes insinuate themselves into and between the maternal cells. . . ." Hence it can be seen that in each of the three lizards *C. tridactylus*, *L. entrecasteauxi* and *T. scincoides* the foetus obtains its food by the glandular activity of the uterine epithelium and the absorbing and phagocytic powers of the chorionic ectoderm. In other words it is the epithelial tissues which play the important part in food transition (Text-fig. 1, A).

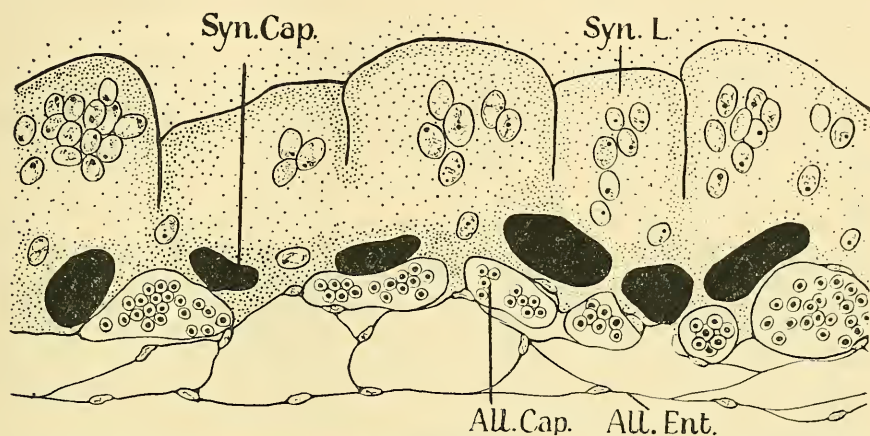
This is a distinct type of allantoplacentation and it differs from that existing in *L. quoyi* since in the one, the epithelial tissues are modified to perform the function of food transition, while in the other the epithelial tissues partially degenerate to allow the maternal capillaries to pass maternal materials more or less directly to the foetal capillaries (Text-fig. 1, B). The relationship which exists between these two types of placentation is somewhat similar to that which exists between the indecidualate and decidualate types of mammalian placentation, although the difference which occurs between the two reptilian types is not as great as that which occurs between the two mammalian types. The placentation of *C. tridactylus*, *L. entrecasteauxi* and *T. scincoides* resembles the indecidualate form of mammalian placentation in essentials, allowance being made for the comparatively simple structure of the reptilian uterus and the difference in the sizes of the developing embryos. The placentation of *L. quoyi* resembles that of the three above mentioned lizards in that there is no invasion of maternal tissue but in other respects it resembles the decidualate mammalian type.

### 3. COMPARISON WITH THE MAMMALIA.

*Perameles* is the only marsupial for which allantoplacentation has been recorded. The placentation of *Perameles* was described by Hill (1897), redescribed by Flynn (1923), and these authors hold different opinions as to the nature of the placenta. Hill claims (1897, p. 387) that the uterine mucosa undergoes hypertrophy; that the vessels in the mucosa increase in size and number; that the uterine epithelium changes into a vascular syncytium, the nuclei becoming grouped together in nests situated in lobular projections of the deeper surface of the syncytium; and that the maternal corpuscles pass up between the syncytial lobules and form a network beneath the epithelial protoplasm. He claims further that the embryo becomes attached to the prepared maternal wall by means of enlarged chorionic ectoderm cells, which eventually degenerate over the placental area proper; that the allantoic capillaries now directly reach the vascular surface of the maternal placental syncytium to which they become intimately attached, dipping down into the depressions on its surface and forming in places a regular

interlocking system, and that finally the foetal and maternal blood streams are now only separated by their thin endothelial walls and perhaps a layer of syncytial protoplasm (Text-fig. 2).

Flynn claims (1923, p. 175) that the chorionic ectoderm does not completely degenerate but actively invades the maternal tissues and thus brings the type of placentation found in *Perameles* in line with that found among the eutherian mammals, more especially the Carnivora "where there are the same characteristics of passivity of uterine epithelium and activity of the trophoblast with a division of the latter into a cytotlastic and plasmodial layer".



Text-figure 2.—Section through allanto-placental region of *Perameles* (after Hill). All. Cap., Allantoic Capillary; All. Ent., Allantoic Endoderm; Syn. Cap., Syncytial Capillary; Syn. L., Syncytial Lobule.

However both authors agree that the foetal membranes of *Perameles* are closely apposed to the maternal wall and that a degeneration of epithelial tissues leads to a close proximity of maternal and foetal blood streams, a condition of affairs hitherto only met with among the Eutheria. But it will be recalled that in *L. quoyi* there is the same partial degeneration of epithelial tissues and mutual apposition of maternal and foetal blood streams, and further that this is the only recorded case among reptiles of this type of allanto-placentation. Hence the deduction that the allanto-placentation of *L. quoyi* more closely resembles that of the Mammalia, than any hitherto recorded in a reptile.

#### 4. THEORETICAL CONSIDERATIONS.

As this is a preliminary communication, it is unnecessary to enter upon a lengthy discussion of the significance of the allanto-placentation of *L. quoyi*, yet the type of placentation is so interesting and its bearing upon phylogenetic questions of such importance that a brief discussion of the outstanding features of interest is warranted.

The importance of the nature of the allanto-placentation in *L. quoyi* is indicated when it is demonstrated that in the genus *Lygosoma* two members, namely *L. entrecasteauxi* and *L. quoyi*, have each developed distinct types of placentation between which there is almost as much difference as exists between the

indeciduate and deciduate mammalian types (Text-fig. 1 A, and B). The occurrence of these distinct types of placentation in two members of the same genus is, to my mind, conclusive evidence of the independent evolution of the placenta in each. Hence I now claim that besides the three lizards *C. tridactylus*, *T. scincoides* and *L. entrecasteauzi*, a fourth lizard, *L. quoyi*, has independently developed an allantoplacenta, a fact which further strengthens the suggestion in a previous paper on lizard placentation by Harrison and Weekes (1925, p. 484), that "the occurrence of true placentation in two not very closely related Scincid lizards *Lygosoma* and *Chalcides*, in Australia and Europe respectively, indicates that the allantoplacenta is a functional adaptation, which may have arisen independently many times in evolution and upon the mere occurrence of which phylogenetic statements cannot justifiably be based".

In his account of the placentation of *Perameles*, Flynn says (1923, p. 127), that "according to Hill's account the placentation of *Perameles* is without parallel in the whole mammalian group" and he adds that this fact has led even Hubrecht to suggest (1909) that the placenta of *Perameles* on further investigation may after all prove to be more comparable with some one or other of the placentae of the Eutheria. Flynn studied the placentation of *Perameles* with the object of discovering, if possible, some link between it and the eutherian type and he claims that his investigations revealed satisfactory results, the placentation of *Perameles* being comparable to some extent with that found among the Carnivora. But since two essentially dissimilar types of allantoplacentation occur in two members of the reptilian genus *Lygosoma*, and further, since there is a much closer relationship between these two members than exists between the marsupial and eutherian mammals, I suggest that the fact that the placentation of *Perameles* as described by Hill may have "no parallel among the whole mammalian group" need not be as incredible as Hubrecht and Flynn suppose.

It will be recalled that in *L. quoyi* the chorionic ectoderm of the placental region is inactive and partially degenerates after the fixation of the embryonic membranes, allowing for a close proximity of maternal and foetal capillaries. Since such a specialized type of placentation has presumably been independently evolved in this viviparous lizard from oviparous stock as an adaptation to environment, I venture to suggest that the somewhat similar placental condition in *Perameles* (after Hill) may be the result of a similar response to environment and may be independent of any genetic relationship with that of the Eutheria.

##### 5. SUMMARY.

(a) Omphaloplacentation and allantoplacentation are recorded for the viviparous Scincid lizard *Lygosoma (Hinulia) quoyi*, the type of allantoplacentation being compared and contrasted with that of the Reptilia and the Mammalia.

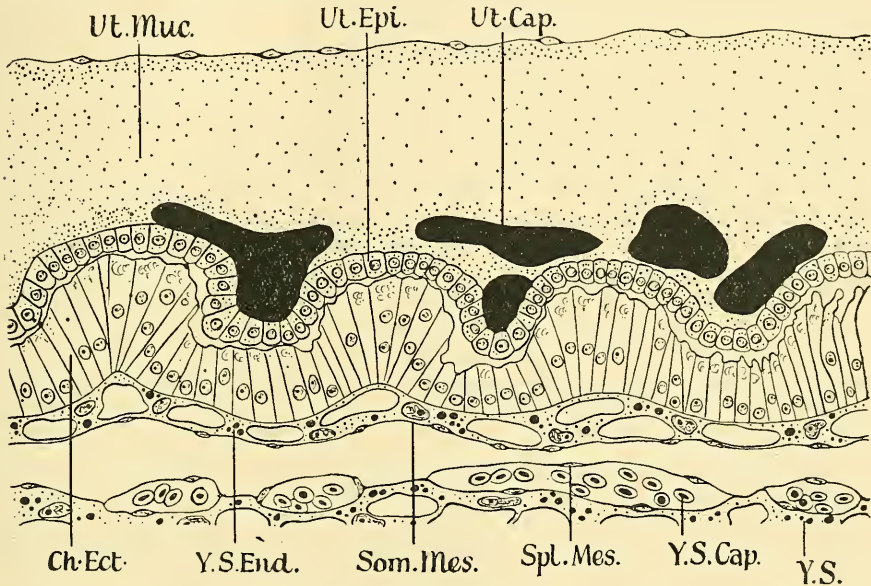
(b) The occurrence of two distinct and dissimilar types of allantoplacentation in two species of one reptilian genus indicates that the allantoplacenta is a functional adaptation evolved independently in each species.

(c) The difference between these two types of allantoplacentation in two closely related lizards emphasizes the fact that a similarity between the marsupial and eutherian types of allantoplacentation need not necessarily be expected.

(d) The similarity between the independently developed allantoplacentation of the specialized reptile *L. quoyi* and that of the specialized marsupial *Perameles* (after Hill) suggests that a similar response to environmental conditions has occurred in these widely separated forms.

II. ON THE PECULIAR GROWTH OF THE EXTRA-EMBRYONIC MESODERM IN  
*Lygosoma (Hinulia) quoyi*, *Tiliqua scincoides*, *Egernia whitei*  
AND *Egernia striolata*.

In each of the above mentioned lizards the growth of the extra-embryonic mesoderm is normal until the formation of a temporary sinus terminalis. The mesoderm then dips into the yolk-sac and continues its growth, not over the surface of the latter as is normally the case, but embedded in its substance. As the mesoderm grows into the yolk-sac it splits into two layers as it does in the normal condition when forming the extra-embryonic coelome. Thus an outer layer of endoderm is separated from the bulk of the yolk-sac, a condition not hitherto recorded (Text-fig. 3, Y.S. End.).



Text-figure 3.—Section through omphaloplacental region of *T. scincoides* showing apposition of chorionic ectoderm to maternal villous ridges. Ch. Ect., Chorionic Ectoderm; Som. Mes., Somatic Mesoderm; Spl. Mes., Splanchnic Mesoderm; Ut. Cap., Uterine Capillary; Ut. Epi., Uterine Epithelium; Ut. Muc., Uterine Mucosa; Y.S., Yolk Sac; Y.S. Cap., Yolk Sac Capillary; Y.S. End., Yolk Sac Endoderm.

III. ON THE OCCURRENCE OF CORPORA LUTEA IN *Lygosoma (Hinulia) quoyi*,  
*Tiliqua scincoides*, *Egernia whitei* AND *Egernia striolata*.

After ovulation the ruptured follicles in the ovaries of each of the four above mentioned lizards become yellow in appearance and richly vascular. This is due to the presence of a corpus luteum in each, the growth of which is rapid, each follicle being completely filled with luteal cells in less than a week after ovulation.

IV. THE OMPHALOPLACENTA OF *Tiliqua scincoides*.

Flynn (1923) described the occurrence of an allantoplacenta in *T. scincoides* but made no mention of an omphaloplacenta. The presence of an omphaloplacenta in this lizard is now recorded (Text-fig. 3).

Both immature and mature stages in the development of the omphaloplacenta are available, the placenta apparently functioning throughout the development of

the embryo. The area of placental modification extends over the entire under surface of the yolk-sac where the bounding layer of chorionic ectoderm comes into contact with the surrounding uterine wall.

The uterine wall and the chorionic ectoderm are thrown into a series of folds which interlock, recalling the attempt at the formation of an omphaloplacenta in *C. tridactylus* and *C. ocellatus* (Giacomini, 1891 and 1906 respectively), and the type of omphaloplacenta found in the marsupial *Didelphys* (Selenka, 1886; Osborne, 1888). The folded wall of the uterus is thickened over the placental region and is lined by enlarged epithelial cells containing large, deeply staining nuclei. The chorionic ectoderm consists of extremely narrow elongated cells which fit into the maternal crypts, there being no actual interpenetration of maternal and foetal tissues. The arrangement of the foetal tissues surrounding the yolk-sac is not usual owing to the peculiar growth of the extra-embryonic mesoderm mentioned above. Beneath the chorionic ectoderm there is a thin layer of yolk-sac endoderm containing yolk granules. Between this and the main yolk-sac is the extra-embryonic mesoderm which has differentiated in the normal manner into somatic and splanchnic layers. The somatic mesoderm together with the above mentioned layer of yolk-sac endoderm and chorionic ectoderm is separated from the yolk-sac, and it is this band of tissue which is folded to fit into the maternal crypts (Text-fig. 3). The splanchnic mesoderm lines the yolk-sac and gives rise to a complex network of blood vessels which ramify through the substance of the latter.

Detailed accounts of these phenomena are in course of preparation.

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